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Riparian habitat fragmentation and population persistence of the threatened valley elderberry longhorn beetle in central California

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Abstract

We studied regional- and local-scale occurrence of the threatened valley elderberry longhorn beetle (VELB) in central California to further understand population dynamics of this habitat specialist in fragmented riparian woodlands. In 1991 and 1997, we surveyed 65 riparian sites along the Sacramento River and 13 of its tributaries for VELB occurrence by examining elderberry bushes for characteristic emergence holes. We also compared VELB local abundance with that of its more common closest relative, the California elderberry longhorn beetle (CELB). Our research revealed that in the northern half of its geographic range, the VELB occurs in drainages that appear to function as distinct, relatively isolated metapopulations. Survey sites within drainages exhibited turnover in site occupancy between 1991 and 1997, but between-drainage site turnover was rare. Sites that were colonized in 1997 were surrounded by a greater number of occupied sites than those that were not colonized, suggesting that VELB colonization of isolated sites or drainages is constrained by limited dispersal. VELB exit holes consistently occurred: (1) in clumps of elderberry bushes rather than in isolated bushes in both survey years; (2) in elderberry branches 5–10 cm in diameter; and (3) in branches <1 m off the ground. We observed similar patterns of resource use by the VELB and its closest relative, the CELB, but very different patterns of resource availability in their preferred sites. VELB sites had much higher elderberry densities, but lower exit hole densities, than did CELB sites. We suggest that conservation and restoration strategies must consider the details of metapopulation viability and patch occupancy as well as what constitutes suitable habitat for a species.

Keywords: California elderberry longhorn beetle; Population dynamics; Valley elderberry longhorn beetle; Metapopulations; Riparian woodlands; Habitat fragmentation

1. Introduction

Studies of habitat loss and fragmentation are central to conservation biology (Pimm and Gilpin, 1989; Collinge, 1996; Schwartz, 1997; Harrison and Bruna, 1999), from investigations of regional-scale patterns and processes of landscape change (Edwards et al., 1994; Forman, 1995; Turner et al., 1996) to studies of population dynamics of individual species in fragmented habitats (Lamberson et al., 1992; Pulliam et al., 1992; Doak et al., 1994; Root, 1998). Various spatial patterns of land conversion for human activities (Collinge and Forman, 1998) alter distribution of habitats and resources, which may affect demographic processes including plant dispersal (Robinson et al., 1992; DeFerrari and Naiman, 1994), plant and animal reproduction (Dooley and Bowers, 1998; Groom, 1998; Jules, 1998), and animal movement patterns (Ims, 1995; Andreassen et al., 1998; Collinge, 2000). Many species face extinction due to demographic or environmental stochasticity given current rates of habitat loss, fragmentation, and degradation (Hastings, 1980; Fahrig, 1997; Huxel and Hastings, 1998).

Historically, California's Central Valley was dominated by a mosaic of habitat types, including perennial grasslands, vernal pools, freshwater marshes, and riparian woodlands (Barbour et al., 1993), which have largely been replaced by urbanization and intensive agricultural

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production (Kucera and Barrett, 1995). As a result, habitat for native species has been drastically reduced. Riparian areas, in particular, are complex and diverse ecosystems that have significantly declined in California and throughout western North America (Naiman et al., 1993; Naiman and Décamps, 1997). It is estimated that only 10% of the riparian woodlands present in the Central Valley 200 years ago remain intact (Smith, 1980; Thelander and Crabtree, 1994), largely due to levee construction for flood control, stream channelization, increased residential and commercial development, and agricultural activities. Some of the rarest plant and animal species in both California and much of semi-arid western North America are riparian habitat specialists (Sands, 1980; Patten, 1998). These species are particularly vulnerable to loss and fragmentation of riparian forests.

One such rare, riparian forest specialist is the valley elderberry longhorn beetle (VELB), *Desmocerus californicus dimorphus* Fisher (Coleoptera: Cerambycidae), which occurs in riparian forest patches along the Sacramento, American and San Joaquin rivers and their tributaries in central California (Linsley and Chemsak, 1972; US Fish and Wildlife Service, 1984; Lang et al., 1989; Barr, 1991). In 1980 the VELB was designated by the US Fish and Wildlife Service as a 'threatened' species under the Endangered Species Act (Federal Register, 1980, 1994). Originally described by Fisher (1921), historically this species is believed to have been restricted to an area of ca. 300×100 km in the lower Sacramento and upper San Joaquin Valleys, as small populations in elderberry thickets along river margins (Linsley and Chemsak, 1972; Federal Register 1980, 1994). Hence, VELB populations may be increasingly at risk of extinction due to the destruction and modification of their riparian habitat.

Linsley and Chemsak (1972) recognized two subspecies of *Desmocerus californicus* based on male coloration and geographic range. *Desmocerus c. californicus* Horn, California elderberry longhorn beetle, (CELB) was reported to occur throughout the coastal regions of California, from Mendocino County to Los Angeles County, while *D. c. dimorphus* (VELB) was more narrowly distributed in the Sacramento and upper San Joaquin valleys. Based on Barr's (1991) survey, the VELB's current, known geographic distribution reaches from Redding, CA (Shasta County) at the northern end of the Central Valley, ca. 715 km south to the Bakersfield area (Kern County).

Both the VELB and the CELB are specialist herbivores on blue elderberry (*Sambucus mexicana* Presl: Caprifoliaceae) and red elderberry (*Sambucus racemosa* L. var. *microbotrys* (Rydb.) Kearney and Peebles: Caprifoliaceae) (Hickman, 1993) and the CELB is more common throughout its range than the VELB. Very little is known, however, about the factors that influence the local abundance and spatial distribution of either of these subspecies. In this study, we collected information on both subspecies to increase our understanding of ecological factors that contribute to population dynamics of the threatened VELB.

Island biogeography (MacArthur and Wilson, 1967) and metapopulation theory (Levins, 1969; Hanski and Gilpin, 1997) provide a conceptual framework for studies of species persistence in fragmented habitats (Doak and Mills, 1994; McCullough, 1996). In the context of our study, two key points are relevant. First, if colonization and extinction are related to habitat isolation, as predicted by island biogeography theory, isolated riparian fragments should be less frequently occupied by the VELB than riparian fragments that are close to a source of colonists. Second, metapopulation theory predicts that as continuous populations are converted to disjunct, isolated populations, population dynamics and persistence potentially move toward instability of local populations, but regional stability may still be maintained with appropriate rates of interpatch migration (Harrison, 1994; Holyoak and Lawler, 1996; Hanski and Gilpin, 1997). Hence, examination of VELB populations at both local and regional scales should provide clues to factors influencing population dynamics.

We studied VELB occurrence in riparian habitat fragments in California's Sacramento Valley to further understand factors influencing its distribution and abundance at both regional and local spatial scales. Our goals were to: (1) identify patterns of VELB site occupancy and population turnover over a 6-year period; (2) assess factors that influence local abundance of the VELB; and (3) compare local VELB distribution patterns to those of its more common closest relative, the CELB.

2. Methods

2.1. Study organisms

The VELB is a specialized herbivore that inhabits a highly fragmented landscape. It is endemic to California's Central Valley (Linsley and Chemsak, 1972; Barr, 1991), where populations of beetles occur only in association with their host plants, blue and red elderberry. Blue and red elderberry both occur commonly in riparian forest patches along the Sacramento, American, and San Joaquin rivers and their tributaries (Linsley and Chemsak, 1972; Barr, 1991), and may also be found as isolated bushes or clumps of bushes in elderberry savannas adjacent to riparian vegetation (Sawyer and Keeler-Wolf, 1995). Remnant patches of riparian forest and valley oak woodland (Conard et al., 1980) contain other woody species such as Fremont cottonwood (*Populus fremontii*), California sycamore (*Platanus racemosa*), willow (*Salix* spp), wild grape (*Vitis californica*), blackberry (*Rubus* spp), and poison oak (*Toxicodendron diversilobum*) (US Fish and Wildlife Service, 1984; Sawyer and Keeler-Wolf, 1995).

Adult VELB females lay eggs in cracks or crevices of elderberry stems or on leaves, and the eggs hatch after a few days (Linsley and Chemsak, 1972; US Fish and Wildlife Service, 1984; Halstead and Oldham, 1990). First instar larvae bore into the stems, where they develop for 1 or 2 years (Halstead and Oldham, 1990). During the course of development, larvae create a characteristic feeding gallery in the central pith of the branch (Davis and Comstock, 1924; Lang et al., 1989; Barr, 1991). Shortly before pupation, late-instar larvae chew through the inner bark of the elderberry stem, then move back down the feeding gallery to an enlarged pupal chamber (Halstead and Oldham, 1990). Adults chew through the outer bark and emerge through this exit hole of 4–10 mm diameter during the flowering season of elderberry, mid-March–mid-May (Davis and Comstock, 1924; Linsley and Chemsak, 1972; US Fish and Wildlife Service, 1984). Adults live for a few days to a few weeks (Arnold, 1984; Halstead and Oldham, 1990), mating, and feeding upon the nectar, flowers, and leaves of elderberry. Linsley and Chemsak (1972) suggested that because of their specialized life history and restricted distribution, VELB populations might have always been relatively small.

2.2. Regional-scale surveys

In April–July 1991 and April–June 1997, we conducted regional-scale surveys of the Sacramento Valley for elderberry bushes and VELB presence (Table 1, Fig. 1). The study area spanned 14 drainages in eight northern California counties (Butte, Placer, Sacramento, Shasta, Sutter, Tehama, Yolo, and Yuba), ranging from 38°00′ to 41°00′ N and 122°37′30″ to 120°52′30″ W (Fig. 1). Barr examined 79 sites in 1991, mostly in riparian habitats along the major rivers and streams of the Sacramento Valley (Barr, 1991). In 1997, we resampled 65 of those sites using the same methods (Table 1). We were unable to gain access to seven sites in 1997 that were sampled in 1991, and for an additional seven sites sampled in 1991, elderberry bushes were not present in 1997.

Table 1
Summary of results of eight-county, Sacramento Valley survey for elderberry bushes and VELB site occupancy, April–June 1991 and 1997[a]

VELB surveys	1991	1997
Number of sites surveyed	79	65
Groups of elderberry bushes surveyed	117	111
Individual bushes recorded	No data	818
Number of recent exit holes	31	27
Number of old exit holes	No data	152
Number (%) of sites with recent or old exit holes	29 (36.7)	30 (46.2)
Number (%) of sites with recent exit holes only	16 (20.2)	13 (20.0)

[a] A 'group' consisted of a cluster of one to several elderberry bushes, and at each site, we surveyed from one to three groups of elderberry bushes for VELB exit holes.

At each survey site we estimated elderberry density qualitatively using three categories: 'isolated' sites contained one to a few lone bushes with no others within sight (200–500 m), 'scattered' sites had several bushes spaced 30–50 m apart, and 'clumped' sites had many bushes or clumps, often in large groves. Within each survey site, we randomly selected distinct 'groups' of elderberry bushes to sample for VELB presence. The number of individual bushes per group varied among the three density categories (mean ± SE for clumped sites = 21.7±15.7, scattered sites = 9.4±1.3, and for isolated sites = 3.9±0.5). We carefully searched all branches and trunks in each group of elderberry bushes for VELB exit holes, regardless of site density category. Thus, at clumped sites, we spent more time searching for VELB exit holes, due to the higher number of individual bushes in the groups, than at scattered or isolated sites. Barr (1991) surveyed a total of 117 such groups in 1991 and we sampled 111 groups in 1997 (Table 1). For each group we recorded the maximum diameter of the largest elderberry trunk and noted any damage to elderberry bushes from branch pruning, fire, and herbicide over-spray.

We examined elderberry bushes for evidence of VELB by scanning the foliage, flowers, trunks, and branches for adult beetles, and the branches and trunks for characteristic exit holes (Arnold, 1984; Lang et al., 1989; Halstead and Oldham, 1990, Barr, 1991). With the unaided eye, exit holes and adults could be seen up to a height of 5 m. We also scanned the canopy for beetles using binoculars (Barr, 1991). Adult VELB are rarely observed in the field (Lang et al., 1989; Barr, 1991), so populations are typically censused by counts of exit holes in trunks and branches of elderberry. The VELB is the only insect known to form holes of this type and diameter in the Central Valley of California (Lang et al., 1989). In rare circumstances there was doubt regarding the origin of the hole, so we did not attribute the hole to the VELB.

We determined if holes were recent or old by illuminating the hole interior with a flashlight. The presence of frass, wood shavings, and light-colored wood inside the hole were used as evidence of recent holes (Linsley and Chemsak, 1972; US Fish and Wildlife Service, 1984; Lang et al., 1989; Barr, 1991). Recent holes are likely from adult emergence during the current year (Lang et al., 1989; Barr, 1991). All other holes were recorded as old. When an exit hole was located, we recorded the branch diameter at the exit hole, the vertical height of the hole from the ground, and the condition of the wood (live or dead) at the exit hole.

2.3. Local scale sampling

In June and July, 1997, we sampled and mapped the locations of all elderberry bushes and all VELB exit holes in ten, 50×50 m plots in two Sacramento Valley drainages (Putah Creek, $n=6$ sites and American River, $n=4$ sites). We mapped locations of each elderberry

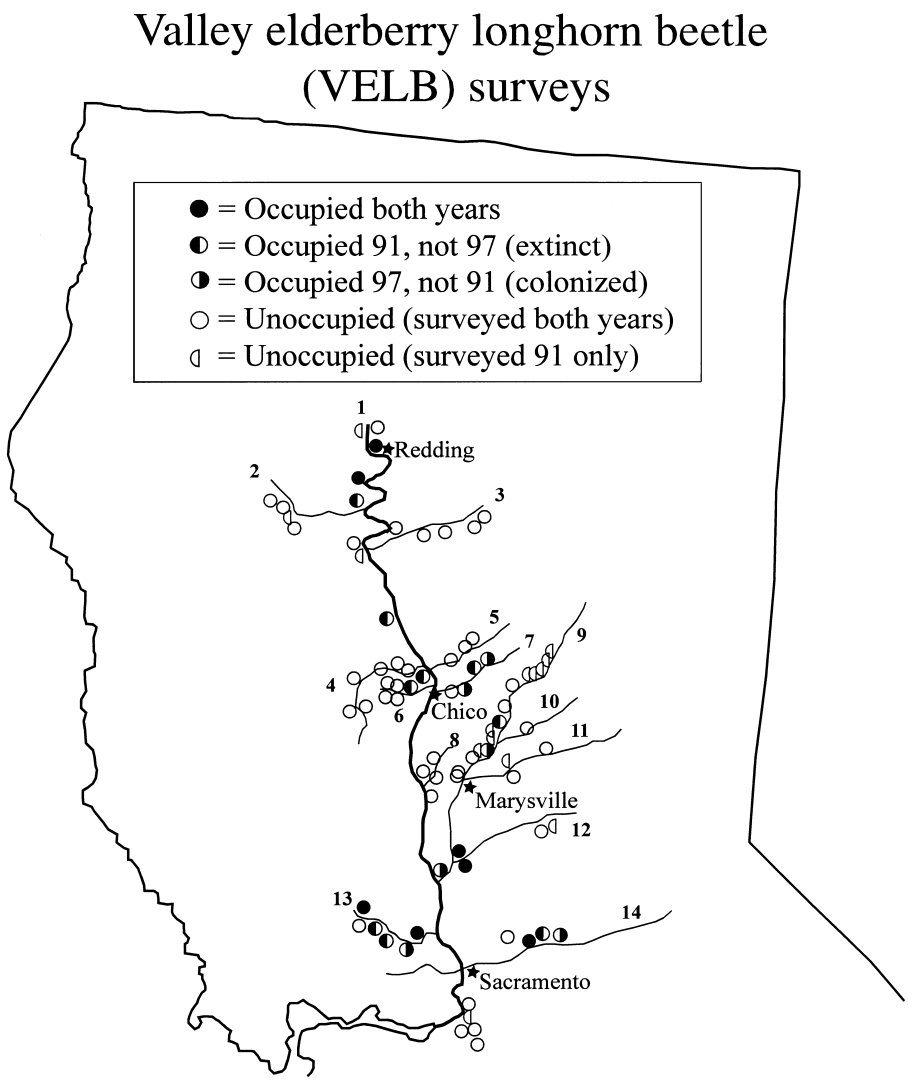

Fig. 1. Map of Sacramento Valley, California, USA, showing distribution of drainages, survey sites, and site occupation indicated by presence of recent exit holes. Dark central line represents Sacramento River, lighter lines indicate the tributaries sampled. Filled circles indicate sites where recent exit holes were observed in both survey years, half-filled circles indicate recent exit holes in one of the years of the survey, open circles indicate sites where recent exit holes were not observed in either year, and half-open circles indicate unoccupied sites that were surveyed only in 1991. Numbers refer to the 14 drainages sampled during the surveys.

bush within the plots using compass readings and tape measures. For comparison with the VELB's closest relative, the CELB, we similarly sampled and mapped CELB distribution on *Sambucus mexicana* bushes in six 50×50 m plots at and near the Hastings Natural History Reservation in Monterey Co., CA (36°12′30″N, 121°33′30″W). As in the regional-scale surveys, for each exit hole we recorded the branch diameter at the exit hole, the vertical height of the exit hole from the ground, and the maximum diameter of the largest elderberry trunk.

2.4. Data analyses

To compare results of the regional scale surveys conducted in 1991 and 1997, we summarized the number of recent and old exit holes at each site and totalled the number of sites unoccupied and occupied in each survey. We used old exit holes as evidence of past occupancy, and recent exit holes as evidence of current occupancy. We mapped survey site locations and compared occupancy within and among drainages in the Sacramento Valley. We computed site extinction and colonization rates in two ways. If a site had exit holes of any age in 1991, but no exit holes of any age in 1997, we recorded it as a *long-term* extinction event. Conversely, if a site had no exit holes of any age in 1991, but recent exit holes in 1997, we recorded it as a *long-term* colonization event. For extinction and colonization over the 1991–1997 time period, we estimated *short-term* extinction and colonization as described above but used only recent exit holes. *Long-term* extinctions may underestimate

actual extinction because old holes may indicate the site is occupied, when it is in fact no longer occupied. *Short-term* data may overestimate extinction rates and underestimate colonization rates because only one year of a 2-year life cycle is recorded.

The likelihood that a survey site is occupied by the VELB may depend upon whether adjacent sites are occupied. We used spatial statistics to assess the degree to which sites close to one another were more similar in occupancy status than sites further apart. We quantified the spatial autocorrelation of site occupancy over five distance classes (0–10, 10–20, 20–30, 30–40, and 40–50 km) using join–count statistics (Real and McElhany, 1996). Join–count techniques are appropriate for analyzing the spatial distribution of discrete variables. For this study, each survey site was assigned a discrete value for site occupancy status (occupied or unoccupied), using data for recent exit holes only from the 1997 survey. Therefore, the three possible occupancy combinations or 'joins' for each pair of sites were occupied–occupied, occupied–unoccupied, and unoccupied–unoccupied. In join–count analysis, the number of each join is counted, then compared to the number of each join expected by chance. If sites are spatially autocorrelated, then the number of joins observed in the occupied–occupied category, for example, will exceed that expected due to chance alone. We tested the hypothesis that the observed number of joins occurred by chance by using Monte-Carlo simulation, in which all sites were randomly reassigned locations and the number of joins calculated for each of 1000 simulations.

To further assess spatial relationships among survey sites, we asked whether *short-term* colonization or *short-term* extinction was influenced by the number of occupied sites within 20 km observed in the previous survey. We hypothesized that unoccupied sites located near occupied sites would be more likely to be colonized than unoccupied sites with fewer or no adjacent occupied sites. We chose 20 km as a distance measure because spatial analyses suggested that sites within 20 km were significantly correlated. For each survey site colonized in 1997, we counted the number of occupied sites within 20 km observed in the 1991 survey. We then compared the number of occupied sites within 20 km in 1991 for sites colonized in 1997 to those that remained uncolonized in 1997 using a non-parametric Kruskal–Wallis ANOVA.

We conducted G-tests of independence (Sokal and Rohlf, 1995) for each survey year to assess if the frequency of recent exit holes was dependent upon qualitative estimates of elderberry density at each survey site. Because branch diameter and height data were not normally distributed, we used the non-parametric Kruskal–Wallis ANOVA (Sokal and Rohlf, 1995) procedure to compare branch diameter and height off of the ground at recent exit holes between 1991 and 1997, and report medians for these variables below (see Section 3).

To compare VELB distribution with that of the CELB, we used non-parametric Kruskal–Wallis ANOVA and report medians below because response variables were not normally distributed. We assessed differences between VELB and CELB 50×50 m sample plots in the number of elderberry bushes, recent exit holes, old exit holes, recent and old hole density (number of holes per elderberry bush), branch diameter and height off ground for both recent and old exit holes.

3. Results

Because we sampled 65 of the same sites and used the same methods as Barr (1991), we could directly compare VELB distribution and abundance among survey sites in 1991 and 1997 (Table 1, Fig. 1). In both surveys, the number of adult beetles observed over the 3-month field sampling period was extremely low. Barr (1991) observed two males and two females, all in the southern half of the Central Valley, while in our 1997 survey we observed one male and one female (Collinge et al., pers. obs.).

Barr (1991) observed 31 recent exit holes in her survey of 117 elderberry groups (26.4% of groups), while our 1997 survey found 27 recent exit holes in 111 elderberry groups (24.3% of groups) (Table 1). In 1991, 29 of 79 sites (36.7%) contained recent or old exit holes and 16 of 79 sites (20.2%) contained only recent exit holes. In 1997, 30 of 65 sites contained recent or old exit holes and 13 of 65 (20.0%) sites contained only recent exit holes (Table 1). The number of old exit holes was recorded differently in the two surveys and thus is not directly comparable between years. In 1997 we recorded the presence of old exit holes at each site and counted the total number of old exit holes observed, while in 1991, Barr recorded the presence of old exit holes at each site but only counted a subset of the old exit holes (Table 1). Our observations from field surveys demonstrate that: (1) VELB population densities are extremely low; (2) only about one-fourth of elderberry groups encountered contained recent exit holes, and; (3) only about 20% of riparian sites with elderberry support extant VELB populations.

Including both old and recent exit holes, 31 of 65 sites (47.7%) were recorded as occupied in either one of the two surveys, leaving 34 of 65 sites (52.3%) that were recorded as unoccupied in both surveys. Of the 31 occupied sites (based on the presence of old or recent holes), we found that 25 sites (80.6%) were occupied in both surveys, two sites (6.5%) showed *long-term* extinctions (observed occupancy changed from occupied to unoccupied between surveys), and four sites (12.9%) showed long-term colonizations (observed occupancy changed from unoccupied to occupied between surveys). When extinction and colonization rates were calculated for the

1991–1997 study period using recent exit holes only, nine sites (29.0%) experienced *short-term* extinctions and six sites (19.4%) exhibited *short-term* colonizations. Based on recent exit holes, we also estimate that, on average, 1.7 occupied sites (0.29 extinctions*0.194 colonizations*100%, or 5.6% of sites) would have undergone both extinction and recolonization within the study period, resulting in no net change in patch occupancy.

We refer to a change in site occupancy status between surveys as 'turnover', presumably resulting from an extinction or colonization event. Considering recent exit holes only, 50 of the 65 sites (77%) had the same occupancy status between surveys, and 15 of the 65 sites (23%) experienced turnover between surveys. Interestingly, with one exception, all cases of turnover occurred within, not between, drainages (Fig. 1). In 1991, we observed recent exit holes in seven of 14 drainages, while in 1997, we observed recent exit holes in six of 14 drainages (Fig. 1). The drainages occupied were identical between surveys except for Stony Creek (drainage number 6, Fig. 1), which was occupied in 1991 but not in 1997.

This tendency for sites within drainages to be more similar in occupancy status than sites between drainages was clearly shown in the spatial autocorrelation analysis (Fig. 2). The join–count analysis indicated that sites within 10 km of one another showed a random spatial pattern of occupancy (proportion of simulations with fewer occupied-occupied joins than the observed value <0.500, Fig. 2). Sites 10–20 km from one another and 30–40 km showed significant clustering, however (proportion of simulations with fewer occupied–occupied joins than the observed value >0.950, Fig. 2). Similarly, survey sites that were colonized in 1997 were within 20 km of a significantly greater number of occupied sites than sites that were not colonized (Table 2). We did not observe this pattern for extinction, however. Sites that experienced extinction in 1997 did not differ significantly in the number of occupied sites within 20 km from those sites that did not experience extinction (Table 2).

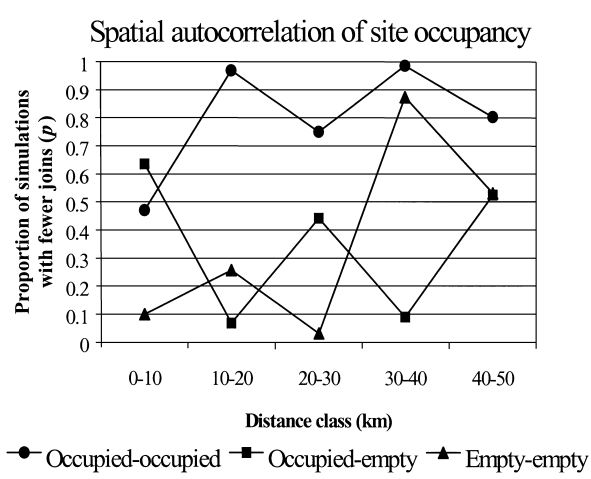

Fig. 2. Results of join–count distance analysis that depicts spatial dependence in occupancy status between sites in relation to linear distance between sites for 1997 VELB survey. The high proportion of occupied–occupied joins at 10–20 and 30–40 km distance suggests that occupied sites are clumped at those spatial scales.

In 1991, VELB recent exit holes occurred disproportionately in sites with clumped elderberry bushes compared to isolated bushes (Fig. 3). The number of sites in the lower density categories, 'scattered' and 'isolated,' increased between 1991 and 1997. Most frequently, sites moved from the scattered to isolated category ($n=17$ sites). It seems unlikely that inter-observer error is responsible for this observation, because 'isolated' was the most unambiguous density category to assign. Regardless, high densities of elderberry bushes are clearly more likely to be occupied than low density sites, but high density sites are the least numerous of the three categories (Fig. 3).

In both survey years, recent exit holes were most frequently encountered in branches 5–10 cm in diameter (Fig. 4a). The median branch diameter in which recent exit holes were found declined significantly from 8.6 cm in 1991 to 6.0 cm in 1997 (Kruskal–Wallis ANOVA, $F_{1,58}=4.40$, $P<0.05$, Fig. 4a). In contrast, we detected no significant differences between the 1991 and 1997 surveys in height of recent exit holes from the ground (Kruskal–Wallis ANOVA, $F_{1,59}=0.07$, $P=0.79$, Fig. 4b). We observed recent exit holes from ground level to 189 cm from the ground (1991 median = 60.9, 1997 median = 58.0).

Finally, VELB exit holes occurred at much lower local densities than did CELB exit holes (Table 3). Despite a nearly seven-fold increase in number of elderberry bushes in VELB versus CELB sample plots, there were nearly five-fold fewer recent VELB exit holes per plot than recent CELB exit holes. Interestingly, the number of old exit holes did not differ significantly among subspecies (Table 3). Branch diameter and height off ground at recent exit holes were similar for the two subspecies, possibly reflecting similar resource

Table 2
Results of non-parametric ANOVA that compared number of occupied sites in 1991 within 20 km of sites colonized (or extinct) in 1997 to number of occupied sites in 1991 within 20 km of sites not colonized (or not extinct) in 1997; sites colonized in 1997 had a significantly greater number of sites occupied in 1991 within 20 km than did sites that were not colonized

	Median occupied sites within 20 km	F	P
Extinct in 1997	1.0	0.63	0.44
Still occupied in 1997	1.0		
Colonized in 1997	1.0	8.59	<0.01**[a]
Still unoccupied in 1997	0.0		

[a] $**p<0.01$.

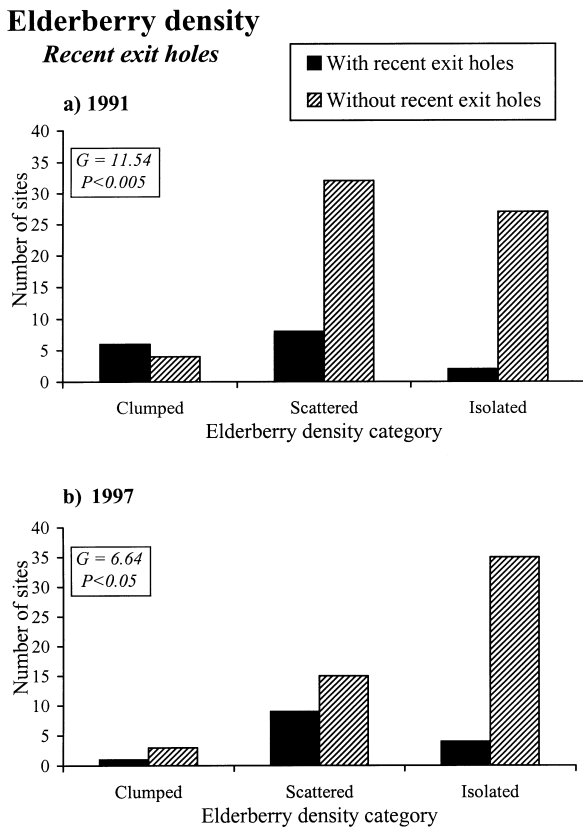

Fig. 3. Occurrence of VELB recent exit holes in relation to elderberry density for (a) 1991 VELB survey and (b) 1997 VELB survey. Solid bars represent sites with recent exit holes; hatched bars indicate sites without recent exit holes. Significant G-tests in both surveys indicate that frequency of recent exit holes is strongly dependent upon elderberry density.

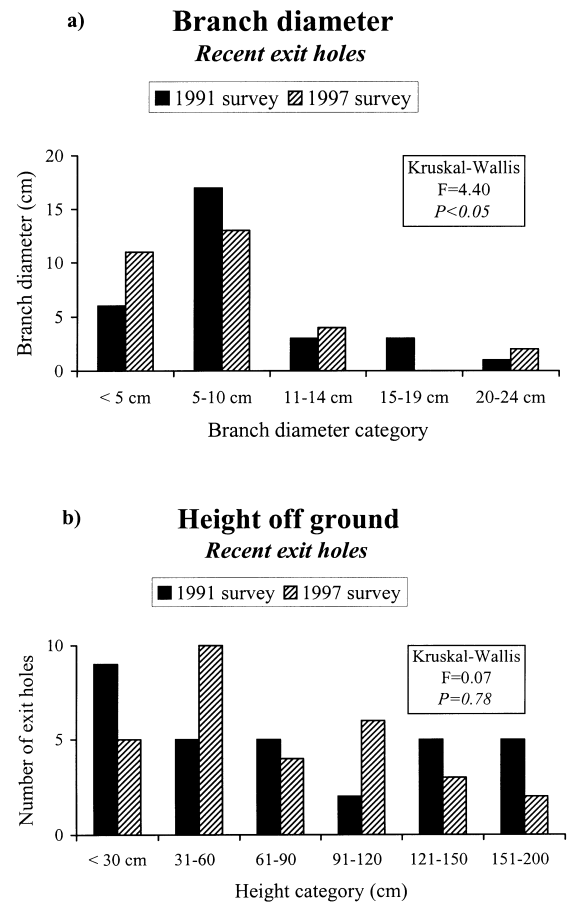

Fig. 4. Occurrence of VELB recent exit holes in relation to (a) elderberry branch diameter and (b) height off ground for both survey years. Solid bars represent number of exit holes in 1991 survey, hatched bars represent number of exit holes in 1997 survey, in each branch diameter or branch height category.

use patterns. These parameters differed significantly for old exit holes, however, with CELB holes occurring in branches of significantly greater size and at greater heights from the ground (Table 3). In sum, the VELB and CELB comparison indicated that occupied elderberry bushes in the CELB's geographic range tend to occur in lower densities, but are of much greater size than those in the VELB's geographic range, and confirmed that the VELB is rarer than the CELB in these sites.

4. Discussion

Our study of the VELB in the northern half of its geographic range revealed that this riparian specialist occurred in drainages that appear to function as distinct, relatively isolated metapopulations. The majority of survey sites (52.3%) that we sampled remained unoccupied in both years of the survey. For occupied sites, *long-term* extinctions (two sites) occurred less frequently than *long-term* colonizations (four sites). With one exception, all site turnover between the 1991 and 1997 surveys occurred within drainages (Fig. 1). Between-drainage site turnover was rare, at least over the 6-year extent of our study. This pattern of site occupancy is intriguing for both conservation and restoration of riparian habitat for the VELB and other riparian specialists, and may be explained by at least three possible mechanisms. First, turnover within, but not between drainages may be a consequence of limited VELB dispersal among drainages. Second, differences in environmental suitability among drainages may limit VELB occupancy of particular drainages. Or third, it may be less likely to detect turnover of entire drainages than turnover of individual sites within drainages. Our evidence tends to support the explanation of limited VELB dispersal among drainages and may indicate the spatial scale at which naturally occurring metapopulations of this species function under field conditions.

At the scale of adjacent survey sites within drainages (sites 0–10 km apart), VELB occupancy of sites appears randomly distributed (Fig. 2), and may be influenced by local processes such as predation, plant quality or intraspecific competition. Recent field observations

Table 3
Median values of elderberry abundance and maximum diameter, and VELB and CELB exit hole abundance, density, and relation to branch diameter and height off ground in 50×50 m plots along Putah Creek and the American River (VELB) and at Hastings Natural History Reservation (CELB)[a]

Variable	VELB[b] Median	CELB[c] Median	F	P
Elderberry bushes per plot	26.5	4.0	13.46	<0.005
Maximum diameter of bush (cm)	26.0	41.5	3.52	0.08
Recent exit holes	0	4.5	11.54	<0.005
Old exit holes	6.5	16.0	1.19	0.29
Recent holes per bush	0	1.5	13.46	<0.005
Old holes per bush	0.39	3.17	7.40	<0.05
Recent holes:				
Branch diameter (cm)	7.0	8.0	1.21	0.28
Height above ground (cm)	76.0	71.0	0.05	0.99
Old holes:				
Branch diameter (cm)	6.5	8.0	10.64	<0.005
Height above ground (cm)	63.0	85.0	8.16	<0.005

[a] ANOVA results are non-parametric Kruskal–Wallis ANOVA's on rank averaged values.
[b] $n=10$.
[c] $n=6$.

(Huxel, 2000) indicate that the predatory, invasive Argentine ant (*Linepithema humile*, Formicidae) may exclude the VELB from otherwise suitable habitat. Argentine ant occurrence tended to be inversely related to VELB occurrence at 30 study sites within the American River and Putah Creek drainages (Huxel, 2000). Previous published research (Ward, 1987; Holway, 1995) has documented the spatial spread of the Argentine ant along riparian corridors in the Sacramento Valley, and demonstrated that Argentine ants exclude native ants in these habitats. Elderberry tissue quality may also influence VELB occurrence and performance. For stem-boring cerambycids in general, developmental time is inversely related to the nutritional quality of the woody tissue in which they feed (Haack and Slansky, 1987). Further, experimental evidence suggests that stressed elderberry bushes are more attractive to VELB adults than non-stressed plants (Arnold, 1984). Finally, it is doubtful that intraspecific competition strongly affects VELB distribution and abundance, given the very low observed densities of recent exit holes at survey sites.

At larger spatial scales, such as across drainages (sites 10–20 and 30–40 km apart), VELB occupancy is clustered, and appears to be more strongly influenced by regional processes such as colonization and extinction. Our survey data indicated that occupancy of particular drainages is highly aggregated and is relatively constant through time, at least during the 6-year period we examined. Moreover, sites that were colonized between 1991 and 1997 were surrounded by a significantly greater number of occupied sites than sites that were not colonized. These combined results suggest that limited dispersal may constrain VELB colonization of isolated sites or drainages.

There appears to be no obvious relationship between VELB occupancy of drainages and factors such as location of drainage within the Sacramento Valley (e.g. west or east side of valley, north or south end of valley, Fig. 1) or elevation. Stony Creek, the one drainage for which occupancy status changed between surveys, is located in the central portion of the Sacramento Valley and does not differ markedly from other drainages. All creek systems surveyed are surrounded by intensive cultivation agriculture, and most are bounded by levees to control flooding.

Harrison and Taylor (1997) noted that many types of spatially structured populations occur in nature, but not all conform to the dynamics predicted by Levins (1969) metapopulation theory. They discussed five metapopulation types, ranging from the 'classic' Levins' metapopulation where all habitat patches are subject to extinction, but are equally likely to be recolonized, to 'non-equilibrium metapopulations', where habitat patches are so isolated from one another that recolonization does not typically follow extinction. This 'nonequilibrium' case may be a more likely outcome when habitat is lost or fragmented by human activities.

In this theoretical context, our data on VELB site occupancy and turnover is consistent with 'classical' (Levins 1969, Harrison and Taylor, 1997) metapopulation dynamics at spatial scales < 20 km. It may be wrong to assume, however, that all habitat within drainages is equally usable. In contrast, these clusters of sites within drainages appeared to be relatively isolated from other drainages, and may function as 'nonequilibrium metapopulations' (Harrison and Taylor, 1997). Our results suggest that Sacramento Valley drainages that are unoccupied by the VELB remain so; they are not likely to be recolonized following extinction. This finding is particularly troublesome for VELB conservation efforts, because it suggests that there may be little chance of natural population recovery following population declines.

Other regional-scale population studies have shown that a variety of population spatial structures may exist within a single species' geographic range (Stith et al., 1996). For example, Florida scrub jay *Aphelocoma coetulescens* population structures and dynamics vary substantially across central Florida, depending upon the spatial distribution of suitable habitat patches and proportion of sites occupied by the jay. Stith et al. (1996) inferred mainland–island metapopulation dynamics in interior Florida, non-equilibrium metapopulation dynamics in the north Gulf coast, and classical metapopulation dynamics in central Florida. The authors' recommended conservation strategies thus varied significantly among these clusters of habitat patches.

Organisms often exhibit distinct patterns of abundance across their geographic range, with greatest

abundance in range centers and lowest abundance at range margins (Whittaker, 1956; Brown, 1995). This spatial variation in abundance may be due to corresponding variation in habitat quality across the geographic range, or to limited dispersal to range edges. Our survey encompassed the Sacramento River and 13 of its tributaries in the northern Central Valley (Fig. 1). We purposely sampled only representative sites along the Sacramento River, because other researchers conducted VELB surveys there in 1985–87 (Lang et al., 1989), and our study was originally designed to examine the extent of the VELB's geographic range (Barr, 1991). Lang et al.'s surveys in the mid 1980s searched 183 miles of the Sacramento River, from its confluence with the American River in Sacramento to just south of Red Bluff, CA. They recorded VELB exit holes at 64% of their survey sites, which is much higher than the 20% we recorded in our surveys. They observed strong spatial variation in exit hole abundance, however; 28% of sites between Sacramento and Colusa (southern portion of survey sites) contained exit holes, while 94% of sites from Chico to Red Bluff (northern portion of survey sites) contained exit holes (Lang et al., 1989). They attributed this variation to differences in land management among these two portions of the Sacramento River, noting that in the southern portion, the extensive flood control system constrains riparian vegetation to very thin strips immediately adjacent to the river.

Our surveys, combined with the Sacramento River survey cited above, are consistent with expectations regarding spatial variation in abundance. If we consider the VELB's range to be a narrow ellipse, with the Sacramento River as the range center and the far reaches of its tributaries as the range edges (Fig. 1), then it is clear that most occupied sites occurred near the geographic range center, along the Sacramento River.

Two primary hypotheses set forth to explain spatial variation across a species geographic range are: (1) higher habitat availability or quality at range centers versus edges (e.g. Brown, 1995) and; (2) limited dispersal of organisms to range margins (e.g. Hanski, 1982). Our data are consistent with a limited dispersal explanation, based on the following reasoning. First, VELB exit holes occurred disproportionately in higher density elderberry stands, suggesting that host density influences site quality. Sites with isolated elderberry bushes, however, were not necessarily more distant from the range center than were clumped sites (Collinge et al., unpub. data). Moreover, in the Sacramento Valley, lower elevation sites closer to the Sacramento River should have lower habitat quality than higher elevation sites more distant from the river, because of increased cultivation agriculture at lower elevations. As a result, habitat quality does not necessarily decline systematically with distance from range center. Second, our site occupancy and turnover data suggest that VELB dispersal among drainages is rare, or at least less common than dispersal within drainages. This observation supports the notion that dispersal limitation prevents the VELB from colonizing unoccupied drainages.

We observed consistent local resource use patterns of the VELB in relation to elderberry density, branch diameter, and height off of the ground. Recent exit holes occurred in clumps of elderberry bushes rather than in isolated bushes in both survey years. The size of elderberry branches occupied was consistent with observations of Lang et al. (1989), with 5–10 cm diameter stems most often containing exit holes. The height off the ground at which VELB emergence holes occurred was consistent among survey years (Fig. 3b) and was similar to Lang et al.'s observations.

We observed similar patterns of resource use by the VELB and its closest relative, the CELB, but very different patterns of resource availability. VELB sites had much higher elderberry densities, but lower exit hole densities, than did CELB sites. CELB recent exit holes tended to occur in similar branch sizes and heights as VELB exit holes. These data suggest that resource quantity does not limit local population densities of the VELB, but perhaps resource quality, presence of natural enemies, limited dispersal, low site occupancy within the region, or anthropogenic disturbances, such as pesticide drift and pruning, restrict VELB densities relative to CELB densities. Anthropogenic disturbance is also clearly greater in the intensively agricultural Sacramento Valley than in the central Coast Range.

The observed pattern of VELB distribution and abundance constitute an unusual 'form of rarity' (Rabinowitz et al., 1986). The VELB has a narrow geographic distribution, the Central Valley of California. It is a specialist on elderberry, which is a riparian or riparian–upland transition species and it appears to have small local populations wherever it occurs. Barr's (1991) survey recorded only four adults and an average of 1.9 recent exit holes per site, and in the 1997 survey, we observed two adults and only 2.1 recent exit holes per site. In contrast, most rare species have large local populations in at least a portion of their geographic range (Rabinowitz et al., 1986). Given the myriad of negative influences encountered by organisms in small populations, such as reduced genetic variability (Lande and Barrowclough, 1987), demographic stochasticity, and Allee effects (Groom, 1998), how likely is long-term VELB persistence?

Because of the difficulties in assessing factors that influence population growth rates of rare species, we recently employed a modeling approach (Huxel and Collinge, unpublished) to examine the effects of various demographic parameters and management strategies on long-term VELB persistence. We found that without reversing habitat loss through habitat restoration, VELB persistence over the next 100 years is unlikely. Habitat restoration may not enhance long-term persistence,

however, unless mitigation sites are placed in close proximity to sites where the VELB occurs naturally (Huxel and Hastings, 1999, Huxel and Collinge, unpublished). Our survey data showed that dispersal among drainages is relatively rare, thus the placement of mitigation sites within the dispersal range of the VELB is crucial. Long-term persistence of this rare species will require prudent choice of mitigation sites, as well as more stringent restrictions on loss of riparian habitat in the Sacramento Valley.

Our observation of spatial dependence of site colonization suggests caution in allowing further destruction of sites that contain the VELB. Decisions regarding placement of mitigation sites should consider the proportion of sites that are occupied within a 20 km distance. Moreover, our data indicate a minimum size or age of elderberry required for VELB usage. The presence of a preference for certain branch diameters could create a time-lag between habitat destruction for development and when mitigation sites offer habitat that is both of a suitable size and likely to be reached by colonists. While the importance of habitat spatial configuration has been extensively explored by conservation biologists, restoration projects are usually aimed at the scale of a particular site and do not consider the important demographic contributions of other restoration sites and nearby native habitats. We suggest that future mitigation plans need to consider not only what constitutes usable habitat for a species, but also the details of metapopulation viability and patch occupancy.

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